Chapter 21

The Biology of Skeletal Populations: Discrete Traits, Distance, Diet, Disease, and Demography

Sorting human from nonhuman skeletal remains and identifying the remains by element, side, age, and sex are generally the most important contributions the osteologist can make to archaeological research. Such identifications, far from being trivial, are often critical in answering archaeological questions. Additional information, however, can often be obtained from skeletal populations. This information can be crucial in reaching a fuller understanding of the past. The reconstruction of population biology from skeletal remains is an activity that involves potential pitfalls as well as potential benefits for the osteologist.

The aims of **paleoepidemiology** (the study of disease in ancient communities) and **paleodemography** (the study of vital statistics in ancient communities) are to gain knowledge about past populations based on the characteristics of subsets of those populations, including those for whom skeletal remains were recovered. As Waldron (1994, 2007) notes, four extrinsic factors act on dead populations, all reducing the size of the subset available for study. These four factors are extrinsic in the sense that they are independent of the biological features of the cemetery population under study. First, only a portion of those who die are buried at the sites being studied. Second, only a portion of those buried evade destruction. Third, only a portion of the undestroyed are discovered. Fourth, only a portion of the discovered are recovered for the osteologist to analyze. With each of these fractionations, the skeletal subset is biased relative to the sample of people in the original population who actually died. Careful evaluation of such potential bias is critical to accurately reconstructing populational attributes of ancient humans.

In the preceding chapters, emphasis was placed on the identification of skeletal parts at the level of the individual. The identifications of individuals and their sex, age, stature, pathology, and idiosyncratic skeletal characteristics can be critically important in forensic, archaeological, or paleontological contexts. In the archaeological context, however, skeletal remains allow us to take additional steps in anthropological analysis. Such analysis aims to elucidate biological parameters of past human populations, including relatedness, diet, disease, and demography. These are areas of human osteology in which research continues at a rapid pace. The reader can keep current in techniques, protocols, and findings through reference to primary research published in journals such as *The American Journal of Physical Anthropology*, *The Journal of Forensic Sciences*, *Forensic Science International*, and *The International Journal of Osteoarchaeology*.

21.1 Nonmetric Variation

One of the first and most important observations that every osteology student makes is that each human skull is different from every other human skull and can be recognized and differentiated on the basis of size, shape, and various bumps, grooves, foramina, or surface textures. Much of this variation may be partitioned according to the factors responsible for it — age, sex, and pathology. However, much of the variation is idiosyncratic and some of it is attributable to ancestry.

Minor variants of the human skeleton were noted by the ancient Greek scholar Hippocrates, who described Wormian bones in human cranial sutures over 2000 years ago. Nonmetric traits (also called **discontinuous morphological traits**, **epigenetic variants**, or **discrete traits**) are expressions of the variation observed in bones and teeth in the form of differently shaped and sized cusps, roots, tubercles, processes, crests, foramina, articular facets, and other features. El-Najjar and McWilliams (1978), Saunders (1989), and Saunders and Rainey (2008) provide reviews of work on these kinds of features in human osteology. The genetic basis for these traits, particularly nondental ones, remains ambiguous, in large part due to the lack of multi-generational skeletal populations with known pedigrees (Carson, 2006b). Another common complaint concerning the use of nonmetric traits is that their definitions and standards for scoring are inadequate or lacking (Rosing,1984; Donlon, 2000; Hefner, 2009). Tyrrell (2000) reviews many of the assumptions inherent in studies of nonmetric traits.

Although the labels applied to nonmetric variation imply that it is discrete, this is not necessarily the case. As Mizoguchi (1985) points out, it is rare that nonmetric "traits" are really discontinuous and discrete, even though they are usually scored by osteologists in a nonmetric fashion (as dichotomous presence/absence scores, or as multilevel trait forms). The expression of many of the traits can, indeed, be quantified. Tyrrell (2000) discusses how the influence of a

Figure 21.1 **Dental nonmetric variations.** Note the shoveled incisors on this individual, as well as the misdirected, unerupted (heterotopic) upper canines, which have here resulted in retention of the deciduous canines. The anomaly is bilateral, with the unerupted canine crowns visible through holes in the anterior surface of the maxillae. Prehistoric, California. Natural size.

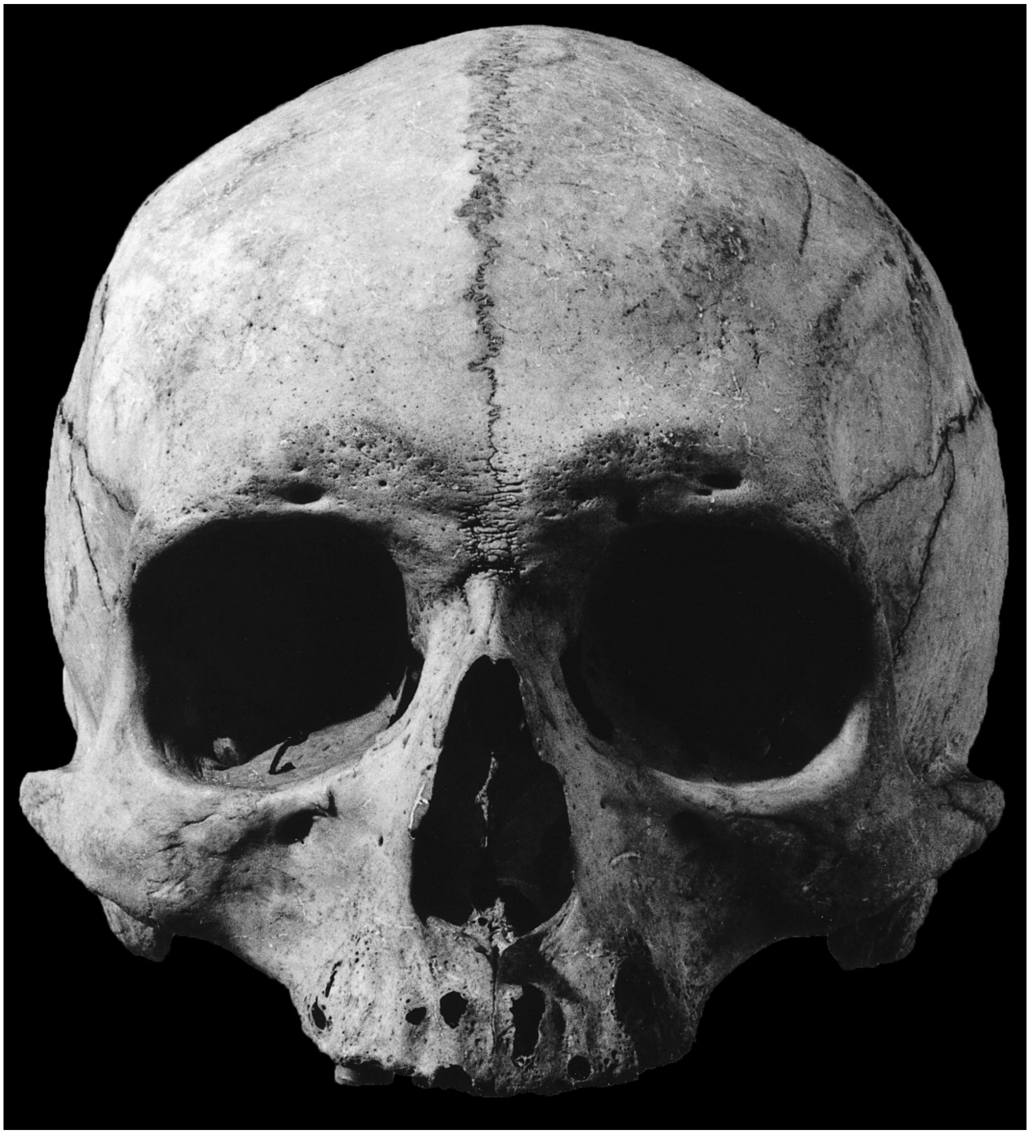


Figure 21.2 **Cranial nonmetric variation.** A metopic suture has persisted into adulthood in this male individual. Prehistoric, North America. Natural size.

developmental threshold on underlying continuous variation can result in dimorphic or polymorphic phenotypic variants that are incorrectly treated as discontinuous variation.

Despite their shortcomings, dental and skeletal nonmetric traits have been shown to be useful in gauging the affinity of extinct human populations. The kinds of nonmetric variation sometimes described in human osteology and used in assessing population affinity are introduced here (for a more complete review of human skeletal nonmetric traits, see El-Najjar and McWilliams, 1978, and Saunders, 1989). Saunders (1989) divides nonmetric traits into eight categories: 1) hyperostotic; 2) hypostotic; 3) foramina/canals/grooves; 4) supernumerary vault sutures; 5) craniobasal structures; 6) spinal structures; 7) prominent bony processes; and 8) facet variations. The Standards volume (Buikstra and Ubelaker, 1994) recommends gathering data for a limited number of "primary" nonmetric traits, and an optional set of "supplementary" traits, both presented in Table 21.5. Some nonmetric skeletal traits, such as the oval window in the middle ear, have proven valuable to forensic osteologists in establishing "racial" affinities of unknown crania (Napoli and Birkby, 1990).

Table 21.1 **Skeletal nonmetric traits***

PRIMARY TRAITS, CRANIAL	SUPPLEMENTAL TRAITS, CRANIAL
Metopic suture	Frontal grooves
Supraorbital notch	Ethmoidal foramina
Supraorbital foramen	Supratrochlear notch or foramen
Infraorbital suture	Trochlear spine
Infraorbital foramen	Double occipital condylar facet
Zygomaticofacial foramina	Paracondylar process
Parietal foramen	Jugular foramen bridging
Sutural bones	Pharyngeal tubercle
epipteric bone	Clinoid bridges or spurs
coronal ossicle	Accessory lesser palatine foramina
bregmatic bone	Palatine torus
sagittal ossicle	Maxillary torus
apical bone	Rocker mandible
lambdoid ossicle	Suprameatal pit or spine
asterionic bone	Divided parietal bone
occipitomastoid ossicle	Os japonicum
parietal notch bone	Marginal tubercle
Inca bone	
Condylar canal	SUPPLEMENTAL TRAITS, POSTCRANIAL
Divided hypoglossal canal	Retroarticular bridge
Flexure of superior sagittal sulcus	Accessory transverse foramen (C3 – 6)
Foramen ovale incomplete	Vertebral number shift
Foramen spinosum incomplete	Accessory sacroiliac articulation
Pterygospinous bridge	Suprascapular foramen or notch
Pterygo-alar bridge	Accessory acromial articular facet
Tympanic dehiscence	Unfused acromial epiphysis
Auditory exostosis	Glenoid fossa extension
Mastoid foramen	Circumflex sulcus
Mental foramen	Sternal foramen
Mandibular torus	Supratrochlear spur
Mylohyoid bridge	Trochlear notch form
	Allen's fossa
PRIMARY TRAITS, POSTCRANIAL	Poirier's facet or extension
Atlas bridging	Third trochanter
Accessory transverse foramina	Vastus notch
Septal aperture	Squatting facets, distal tibia
	Squatting facets, talus
	Talar articular surface (calcaneus)

* Buikstra and Ubelaker (1994) divide traits into "primary" (for which they provide scoring standards) and "supplemental." Their Standards volume provides illustrations and a standard recording form recommended for the compilation of data on the "primary" skeletal discrete traits, as well as references to all of these characters.

21.1.1 Dental Nonmetric Variation

Because teeth are often the most abundant elements in archaeological skeletal series and because tooth size and morphology are often more directly tied to underlying genetics than are other osteological features, teeth have been examined in detail and used widely in osteological analysis. Dental anthropologists use nonmetric variation of tooth crowns to assess biological affinity. Supernumerary teeth, crown fissure patterns, cusp numbers, accessory crown features, and root

number, size, and shape combine with a variety of other traits under the heading of nonmetric dental variation. Dahlberg's casts of dental nonmetric traits, available in many human osteology laboratories, provided a standard for work in this area. The Arizona State University Dental Anthropology System is the current, most widely employed set of standards in dental anthropology (Turner et al., 1991; Scott and Turner, 1997). Figure 21.1 illustrates two nonmetric variants possessed by the same individual. Occasionally there is insufficient space in the jaw for tooth eruption, and **crowding** or **impaction** of teeth are the consequences. These, in turn, can result in pathology of associated soft and hard tissues.

21.1.2 Cranial Nonmetric Variation

A wide variety of nonmetric variants in and between the bones of the skull have been used to differentiate skulls and groups of skulls. A few examples suffice to show the nature of the characters in question: presence or absence of a metopic suture (see Figure 21.2), parietal foramina, extra bones at pterion, wormian bones, multiple mental foramina, and mylohyoid bridges have all been used in nonmetric analyses. El-Najjar and McWilliams (1978) describe 44 such nonmetric traits, Hauser and DeStefano (1989) characterize 84, and Buikstra and Ubelaker (1994) recommend making observations of 21 "primary" cranial nonmetric traits, and list a further 17 "supplementary" cranial nonmetric traits. The traits that Buikstra and Ubelaker consider to be of either primary importance or supplementary are listed in Table 21.1, and details on the scoring of the primary traits are given in Section 4.23.

The importance of cranial nonmetric traits relies on the assumption that these traits are to some extent heritable and can thus be used to investigate ancestry and relatedness. Because of the rarity of skeletal collections of related individuals with known pedigrees, the heritability of nonmetric traits has not extensively tested. In the few studies that have been done (Berry, 1975; Sjøvold, 1984; Carson, 2006b), results have been inconclusive. The effect of cranial deformation on the expression of cranial nonmetric traits has also been investigated as means of determining the degree of environmental plasticity of these traits (Ossenberg, 1970; Pucciarelli, 1974; Konigsberg et al., 1993; O'Loughlin, 2004; Del Papa and Perez, 2007; Van Arsdale and Clark, in press). Del Papa and Perez (2007) found that traits that develop postnatally (*e.g.,* sutural bones) are particularly phenotypically variable, and recommend against their use in studies of biological distance.

Developmental anomalies of the skull, such as scaphocephaly (long narrow skulls caused by premature closure of the sagittal suture), have also been considered by some to represent nonmetric variants. Others simply consider them to be developmental anomalies. A skeletal anomaly is usually considered to be pathological if it is selectively disadvantageous to the individual.

21.1.3 Postcranial Nonmetric Variation

Finnegan (1974) found that estimates of biological distance derived from cranial nonmetric traits were highly correlated with distance estimates derived from postcranial nonmetric traits. He suggested that postcranial nonmetric traits might be better suited to analyses of biological distance in archaeological samples because all of the traits used have the possibility of bilateral expression and because the traits are situated on elements that are often preserved in an archaeological context. Finnegan (1978) made observations of the presence of 30 postcranial nonmetric traits on a skeletal sample of known age, sex and ancestry (Terry collection, see Table 18.1). He found no side dimorphism, and found sexual dimorphism in some traits, but at levels lower than that found with cranial nonmetric traits.

Saunders (1978) examined a set of 50 postcranial nonmetric traits to determine which are best suited to analyses of biological distance. She found small inter-trait correlations within the hypostotic and hyperostotic trait groups, and reported that hyperostotic traits were more commonly present on the right side and in males.

Donlon (2000) examined a set of 40 postcranial nonmetric traits, 32 bilateral and 8 midline traits. Nineteen traits remained after excluding traits related to biomechanical adaptations, traits related to pathological conditions, insufficiently variable traits, and traits with high inter-trait associations. In an analysis of these 19 traits, Donlon found close conformity of biological distances with those obtained from genetic markers, but only for female and pooled-sex samples; results for males did not agree with the genetic distances.

Postcranial nonmetric traits still hold much promise, but more work is required to determine the extent to which these traits have a genetic basis. As a reflection of both the potential of and the problems with postcranial nonmetric traits, Buikstra and Ubelaker recommend the recording of data for only three primary postcranial nonmetric traits, listing a further 19 traits as supplementary.

21.2 Estimating Biological Distance

The assessment of affinity (biological relatedness, usually called biological distance or "biodistance") based on skeletal form has a long history in physical anthropology (Armelagos and Van Gerven, 2003). Larsen (1997) and Mays (2010) provide good reviews of such studies. Osteologists who study the skeletal remains of anatomically modern humans often work on microevolutionary problems. To estimate the degree of biological relatedness between populations, the osteologist works under an important assumption: populations that display the most morphological similarity are the most closely related. The degree to which this assumption is met in practice depends on two major factors: adequacy of sampling, and choice of characters (osteological traits) for comparison (Ubelaker, 1999).

Osteologists observe only samples of biological populations. For osteologists working with archaeological samples, the populations themselves are no longer available for study. Therefore, the strength of osteologically based conclusions about affinity depends on the degree to which the samples accurately reflect the real populations that once existed. The conclusions about relationship can be weakened if the sample is too small or if its composition has been altered in some systematic way. Ubelaker (1999) recommends unbiased adult samples of 100 individuals for each group being compared in biodistance studies. Orton (2000: Chapter 3) gives a good overview of the many assumptions inherent in sampling.

Osteological assessment of the biological distances within and between past populations has traditionally been made on the basis of anatomical traits. These traits should ideally be directly and exclusively controlled by genes. The more susceptible to environmental (including cultural and biomechanical) influence a skeletal trait, the less valuable it is in establishing affinity. For example, flattening of the occipital by the cultural practice of cradleboarding can be observed in distantly related people, but to conclude that two populations manifesting cradleboard-induced occipital flattening were biologically closely related would be misleading. Unfortunately, no single skeletal trait is completely independent of environmental influence.

For several reasons, dentition has been used most effectively to assess relationships between modern and ancient populations. Teeth exhibit a variety of anatomical details that have been demonstrated to be stable through time, to have a high genetic component to their formation, and to differentiate living human populations. Teeth are usually better preserved than bone. In addition, the post-formation effects of environment, gender, and age have less influence on tooth morphology than on most bony anatomy. For these reasons, teeth have figured prominently in reconstructing the biological history of various human populations. Standardization of traits and the methods for scoring them (*e.g.,* Carabelli's effects, fissure patterns, number of cusps, and incisor shoveling) has considerably facilitated and enhanced the accuracy of dental nonmetric analysis (Turner et al., 1991; Scott and Turner, 1997).

Osteologists have traditionally used both metric and nonmetric traits in their assessments of biological distance between skeletal populations (Pietrusewsky, 2008). Multivariate statistics

Table 21.2 **Variation in crown trait occurrence among European American and selected southwestern Native American groups**[a]

		Hopi	Navajo	Zuni	Apache	Mojave	Euro. Amer.
I^1	Shoveling	44.8%	53.7%	47.4%	61.3%	64.6%	0.0%
I^1	Winging	31.4%	23.9%	20.0%	17.2%	32.7%	4.1%
C^1	Tubercle	73.7%	65.6%	90.9%	73.7%	68.4%	72.0%
M^1	Hypocone	84.3%	73.5%	70.5%	83.7%	89.6%	90.8%
M^1	Carabelli's effects	80.3%	61.3%	74.5%	58.3%	72.3%	79.5%
M^1	Cusp 5	18.9%	21.2%	2.9%	15.4%	6.8%	10.4%
C_1	Distal accessory ridge	62.7%	44.6%	79.0%	50.0%	65.0%	21.9%
P_4	Lingual cusp number	15.4%	23.5%	30.4%	17.4%	30.8%	50.9%
M_1	Deflecting wrinkle	37.8%	39.7%	26.0%	66.7%	48.6%	1.8%
M_2	Hypoconulid	76.3%	71.4%	57.1%	63.2%	53.3%	13.1%
M_1	Protostylid	34.4%	35.7%	57.5%	29.2%	25.0%	4.8%
M_1	Cusp 6	49.8%	44.5%	45.2%	56.2%	9.8%	6.1%
M_1	Cusp 7	24.6%	18.4%	22.2%	8.2%	26.8%	24.5%

[a] Data from Scott and Dahlberg, 1982.

such as discriminant functions, principal components analysis, the mean measure of divergence (MMD), and Mahalanobis' distance (d^2) have been employed with metric data, nonmetric data, or a combination of the two, to gauge the biological distance between populations or other groups of people. Such analyses can give insight into questions such as the relative origins (local versus nonlocal) of the victims of Moche ritual sacrifice (Sutter and Verano, 2007), the origins of the ancient Egyptians (Zakrzewski, 2007; Schillaci et al., 2009), or the details of the peopling of the New World (González-José et al., 2005).

The suitability of using nonmetric traits and select metric variables as proxies for genetic markers, and the appropriateness of using distance statistics based on these data as proxies for genetic divergence, rely on a number of assumptions. Several of these assumptions have been examined and tested previously, but the molecular revolution in osteology has now given researchers the means, at least in principle, to directly evaluate osteological biodistance results against genetic distance data. A number of factors (including, but not limited to: cost, bone quality/preservation, contamination issues, and the destructive nature of osteological DNA testing), still militate against the widespread adoption of genetic analyses in osteological analyses (Mulligan, 2005; Kolman and Tuross, 2000; see Chapter 22), but a few studies have included both genetic and osteological biodistance studies.

In one such example, Ricaut et al. (2010) present data on 63 cranial, dental, and postcranial nonmetric traits from 37 adults buried in the Egyin Gol necropolis in Mongolia, for whom genetic analyses had already been undertaken. Using the Mantel test (a correlation statistic), they compare the nonmetric distance matrix to the genetic distance matrix. They find support for the hypothesis that cranial nonmetric traits can serve as an alternative to genetic markers when "detecting outlier group and/or large familial groupings, involving a large number of subjects," but warn that "nonmetric traits do not possess the resolution necessary to detect close genetic proximities between pairs of individuals."

Other biochemical and geochemical analyses are now also being brought to bear on problems of population origin and movement. Some examples include work on the origin and movements of the Alpine Iceman (Müller et al., 2003), on the tracing of slave-trading routes (Schroeder et al., 2009), on commingled remains from Vietnam (Beard and Johnson, 2000), and on the geographic origin of Peruvian trophy heads (Finucane, 2008).

21.3 Diet

One of the primary goals of archaeological research is the reconstruction of subsistence patterns in past human populations. A multidisciplinary approach is usually taken in this endeavor, with specialists analyzing floral, faunal, and fecal material recovered in habitation sites, and still other archaeologists examining the remains of technology used to exploit different food resources. Such an approach uses information from many disciplines to elucidate the past. The osteologist can make contributions to understanding the diet of prehistoric people by examining skeletal pathologies, analyzing dental wear, and by analyzing the relative concentrations of trace and major elements and isotopes extracted from the skeletal remains themselves.

The interaction between nutrition and skeletal pathology is a complex, difficult subject area and the focus of a great deal of current research. For comprehensive reviews of the topic, see Martin et al. (1985), Larsen (1997) and Ambrose and Katzenberg (2000). Indicators such as Harris lines, dental hypoplasia, and craniodental asymmetries may be used on a populational basis to determine nutritional adequacy in prehistory. Unfortunately, however, stress markers in bone are nonspecific, and only patterns and trends of nutritional stress at the populational level can be ascertained. On the opposite end of dietary reconstruction spectrum, the focus can be individual and the results very specific, for example, when colon contents can reveal a meal (Shafer et al., 1989).

21.3.1 Dental Macrowear and Microwear

Dental macrowear (the overall degree of wear on a tooth) has long been used in attempts to characterize prehistoric diet. Teeth interact directly with foodstuffs, and the physical and chemical composition of food has a direct influence on dental macrowear and decay. Prehistoric people who incorporated large amounts of grit into their diet through food-preparation techniques, such as grinding food between stones, exhibit pronounced dental macrowear. The limitations of using dental macrowear to assess diet are easily understood by considering two imaginary prehistoric populations eating exactly the same diet. If one population used sandstone grinding stones to prepare the bulk of its diet, while the other group used wooden mortars, the rate and nature of dental macrowear would be very different, even though the nongrit content of the diet was identical. Smith (1984) and Schmucker (1985) summarized studies aimed at elucidating prehistoric diet through the analysis of tooth wear, and they both found that hunters and gatherers can be distinguished from farmers on the basis of macroscopic tooth wear.

Dental microwear refers to the microscopic traces of wear (pits and striations) seen in the enamel and dentin on the occlusal surfaces of teeth. The exact relationship of dental microwear to dental macrowear is still unclear (Schmidt, 2010). Whereas early approaches to dental microwear were qualitative, the advent of scanning electron microscopy (SEM) made it possible to carefully study and measure microscopic wear on high-resolution, two-dimensional images of teeth (Ungar et al., 2008; Teaford, 1991, 1994, 2000; Walker, 1981). Because of the time and cost involved in SEM studies, researchers have recently re-evaluated the use of low-magnification light microscopy for microwear analysis (Godfrey et al., 2004, 2005; Rivals and Semprebon, 2006). Both SEM and light microscopy rely on counts and measurements of features on two-dimensional images, and have inter-observer error rates of about 9% (Grine et al., 2002). To address the problems of these approaches, researchers are exploring three-dimensional approaches to quantifying dental microwear. Texture analysis uses white-light confocal microscopy to automatically produce a high-resolution three-dimension point cloud for a tooth surface (Ungar et al., 2003, 2008; Scott et al., 2005, 2006). Scale-sensitive fractal analysis (SSFA) is then used to automatically characterize the topography of the point cloud. This and other three-dimensional approaches will continue to be explored as the field of dental microwear matures. Much recent work has focused on the nutritional and other changes associated with the switch to agriculture (Mahoney, 2006; Watson, 2008; Rose, 2008; Deter, 2009). Reinhard and Danielson (2005) ex-

amine coprolites for phytoliths from desert succulents, and caution that the microwear signature of the switch to agriculture is likely to be confounded by continued episodic reliance on traditional hunter-gather staple foods by the earliest horticulturalists.

As with paleopathology, study of dental wear must be done on a populational basis to yield reliable dietary reconstructions. This is particularly true with microwear analysis because the microscopic signature of the individual's last meal or set of meals may not be indicative of what the average diet was over the life of the individual. More research in this area is required, especially with live animals and dental patients (Teaford, 2000). It is clear, however, that dental microwear study is an important complement to macroscopic wear, bone chemistry, and pathological assessment in dietary analysis.

21.3.2 Caries and Calculus

Dental caries also have a long history of inclusion in studies of ancient diets. Unlike dental wear, however, dental caries are a pathological condition whose incidence is under the influence of many factors, including diet. Powell (1985) reviews the use of dental wear and caries in reconstructing prehistoric diet. Lanfranco and Eggers (2010) warn against the using a simple comparison of caries frequencies for inferring dietary differences, and recommend information on caries location, lesion depth, and level of dental macrowear in analyses.

Dental caries is a disease characterized by demineralization of dental hard tissues by organic acids produced when bacteria ferment dietary carbohydrates (especially sugars). Because carious lesions are readily apparent on teeth, there is a very large literature associated with them, even for prehistoric populations. Osteologists have been studying temporal trends in caries since the 1800s. Changes in processing technology and food had important implications for the oral health of past human populations. The incidence of caries has been shown to be generally higher in agricultural than in hunting and gathering economies (*e.g.,* Temple and Larsen, 2007). Cariogenic foods obviously lead to a higher prevalence of caries in a population. Within a population, sex and status differences in the amount of cariogenic food eaten may play important roles in determining the frequencies of caries (Walker and Hewlett, 1990). Larsen (1997) reviews the use of caries frequencies in studies of modern and archaeological skeletal samples.

Several studies (*e.g.,* Hardy et al., 2009; Boyadjian et al., 2007; Henry and Piperno, 2008) have begun to explore the potential of dietary microfossils (starch granules and phytoliths) preserved within dental calculus. Whereas food residues like starch granules can be collected from archaeological tools used to process some foods, these residues are often diagenetically altered. Dental calculus, however, traps phytoliths and starch granules within a concreted matrix, protecting the microfossils from biochemical alteration and allowing for genus- or even species-level identification of the plants from which they derive (Hardy et al., 2009; Boyadjian et al., 2007).

21.3.3 Chemical Analyses

Developments in the chemical analysis of osteological remains have opened new windows on the past. Analysis of trace elements and stable light isotopes in human osteology has played an increasingly important role in dietary reconstruction over the last 30+ years (for reviews, see Price, 1989; Sandford, 1993; Schoeninger, 1995; Larsen, 1997; Sandford and Weaver, 2000; Bentley, 2006; Burton, 2008; Katzenberg, 2008; and Lee-Thorp, 2008).

Traditionally, the issues of diet and affinity have been approached in human osteology via morphological assessment. More recently, however, the application of chemical analyses of osteological remains from archaeological contexts has been added to the osteologist's toolkit. By taking a tiny sample of bone tissue, a researcher can convert the sample into a gas and measure its isotopic compositions with a mass spectrometer. These isotopic ratios can be compared between skeletal individuals, allowing evaluation of subsistence changes through time by direct reference

to the chemical composition of skeletal remains. As Larsen (1997) notes, documentation of diet in the past provides the context for studies of growth, stress, disease, and subsistence activities. Conventional approaches to diet utilized archaeological materials, particularly plant and animal remains. The archaeological record has long been known to be biased in its preservation of food remains, however, and plant remains often approach invisibility due to difficulties in preservation. Having an independent and objective means to generate consumption profiles of different foods eaten in the past is therefore very valuable.

Organisms comprise common elements such as hydrogen (H), carbon (C), oxygen (O), nitrogen (N), calcium (Ca), and less common (trace) elements such as strontium (Sr). Elements can occur as different isotopes, which differ from each other in the number of neutrons they possess. For instance, carbon occurs naturally in three isotopic forms: ^{12}C, ^{13}C, and ^{14}C. Isotopes with too many or too few neutrons (relative to protons) are unstable and prone to decay into lighter, more stable isotopes. ^{14}C is an unstable isotope of carbon whose decay forms the basis of radiocarbon dating. Lighter isotopes (*e.g.,* ^{12}C relative to ^{13}C) break and form chemical bonds more rapidly than heavier isotopes. These facts of chemistry mean that ratios of the stable isotopes can be examined in efforts to deduce aspects of ancient ecology and human behavior, including diet. Carbon and nitrogen are the elements that have received the most attention in studies of human osteological isotopic chemistry, but work is also being done on isotopes of hydrogen (Reynard and Hedges, 2008) and oxygen (White et al., 2004), and it is possible that sulfur may also one day be able to yield paleodietary information (Lee-Thorp, 2008).

Both stable light isotopic forms of carbon (^{12}C and ^{13}C) are found in mammalian bones. The ratio of the heavier isotope (^{13}C) to the lighter isotope (^{12}C) is compared to an international standard ratio. The difference between the ratio found in the sample and the standard ratio is expressed as the isotopic "delta value," or $\delta^{13}C$. The value of $\delta^{13}C$ in mammalian bones reflects diet (*e.g.,* plant tissues consumed during life). Plants use two photosynthetic pathways. The so-called C_3 plants discriminate against the heavier isotope of carbon, and thus their tissues are enriched in ^{12}C. Organisms eating more of these plants will therefore have negative $\delta^{13}C$ values based on their bones. Maize and other C_4 plants do not discriminate as much and have more of the heavier isotope, increasing the ratio of carbon isotopes in the bone collagen of consuming organisms and resulting in positive $\delta^{13}C$ values. Similarly, the heavier ^{15}N isotope of nitrogen concentrates as it travels up through the food chain. Marine plants have higher concentrations of this isotope than land plants, and animals higher up in the marine food chain have, as a consequence, higher $\delta^{15}N$ values in their bones. People feeding on marine mammals are thus expected to have higher $\delta^{15}N$ values than those subsisting on terrestrial food sources. Thus, the isotopic compositions of the bone tissue are useful indicators of diet.

The initial chemical studies of bone (in the 1970s) were received with great enthusiasm because the techniques appeared to provide direct quantitative means for reconstructing diet (Sandford, 1993). By the 1980s, trace element and stable isotope research was heralded as a breakthrough, and more researchers began to conduct these studies. As Sandford (1993) notes, however, the early optimism was soon curbed by studies that demonstrated that elemental concentrations are influenced by many complex and often-interrelated processes. By the late 1980s authors were already referring to the "abuse of bone analyses for archaeological dietary studies" (Hancock et al., 1989) and proclaiming that there were "no more easy answers" (Sillen et al., 1989).

During life, elemental deposition in the skeleton is governed by more than just the abundance of elements in the diet. After burial, bones can be subjected to diagenesis. Concerns over how these variables influence the chemical composition of bone have generated a great deal of additional research. The initial reaction was generally negative, as exemplified by Radosevich's comment (in "The Six Deadly Sins of Trace Element Analysis: A Case of Wishful Thinking in Science," 1993: 318) that: "It is possible that a viable field of trace element analysis of bone in this field can still be constructed, but examinations of basic geochemistry and taphonomy of soil-buried bone must be carried out first, not as an afterthought." Ambrose (1993) agreed in principle, noting that studies of stable isotopes have been developed mostly in geochemistry and plant physiology rather than in anthropology. Nearly two decades of subsequent research has clarified many of

these uncertainties, restoring confidence in isotopic research in anthropology. For example, research has now revealed that the signature of dietary protein is primarily deposited in collagen, whereas the signature of nonprotein dietary components is primarily stored in apatite carbonites (Katzenberg, 2008). Research into improved sampling locations (Jørkov et al., 2009) and extraction methodologies (Jørkov et al., 2007) has also been undertaken. Research is also being conducted to compare the $\delta^{13}C$ and $\delta^{15}N$ values from specific bone collagen amino acids within the same individual as a means of increasing the specificity of identifications of dietary components (Corr et al., 2005; Kellner and Schoeninger, 2007; Naito et al., 2010).

Using analyses of isotopic chemistry, substantial insights into prehistoric diet and land use have been achieved in several areas: the circumstances and timing of the introduction of C_4 plants such as maize (Carpenter et al., 2002; Coltrain et al., 2007); the demonstration that diets of high-status individuals were different from lower-status individuals in some societies (Ubelaker et al., 1995; Linderholm et al., 2008); the exploitation of marine versus terrestrial food sources (Richards et al., 2005); and even the timing of weaning from breast milk (Fuller et al., 2006). Dawson and Siegwolf (2007) and Schwarcz et al. (2010) provide recent overviews of these applications. As with the use of biomolecules in human osteology, stable isotope and trace element analyses require thorough grounding in chemistry, biochemistry, physiology, physics, and other laboratory sciences.

21.4 Disease and Demography

The study of populations, **demography**, is concerned with the vital statistics of populations—life expectancy, mortality rates, birth rates, and population growth, size, and density. Demographers interested in modern people use data collected by census takers who census the living. **Paleodemography** is the study of the demography of prehistoric populations. The vital statistics of these populations can be reconstituted by use of their skeletons. The osteologist can reconstruct these populations by censusing the dead. A major assumption used here by the osteologist is that the rates of growth and aging established for modern humans can be applied appropriately to individuals who lived in the distant past. The more ancient the populations under study, the less valid this assumption is likely to be.

The reliability of demographic reconstructions built on skeletal material depends on the accuracy of individual age and sex estimations of the skeletons. Wittwer-Backofen et al. (2008) demonstrate the difficulties inherent in estimating ages in archaeological material. In addition, their reliability depends on how accurately the sample of skeletons represents what was once the living population. Van Gerven and Armelagos (1983), Greene et al. (1986), Boddington (1987), Bocquet-Appel and Masset (1982), Wood et al. (1992), Jackes (1992, 2000), Konigsberg and Frankenberg (1994, 2002), Chamberlain (2000), Milner et al. (2000), Hoppa and Vaupel (2002), Wright and Yoder (2003), and Bocquet-Appel (2008) provide good reviews of the assumptions and limitations of archaeological data in demographic reconstructions. Figure 21.3 is an illustration of a large cemetery excavated during the 1960s in the midwestern United States. Here, 1327 articulated skeletons were recovered, ranging in age from *in utero* individuals to elderly adults. The excavators estimate that this represents a 300-year occupation (Lovejoy et al., 1985a).

To better understand the constraints and limitations of demographic reconstructions based on skeletal remains, imagine an ancient population in which all of the dead were buried in a single cemetery over the span of 100 years. In this imaginary case, no people died away from home or were cremated or were eaten by carnivores. None of the skeletons were disturbed after burial by biological or physical agents. Furthermore, imagine that the entire cemetery was preserved intact through the centuries. Finally, imagine that all of it was excavated and that all of the individuals, including very young infants, were recovered. Provided that recovery was complete, record keeping was good, none of the skeletal material was lost subsequent to excavation, and the osteologist could accurately age and sex all of the individuals, these data might be used directly to reconstruct demographic attributes of the population.

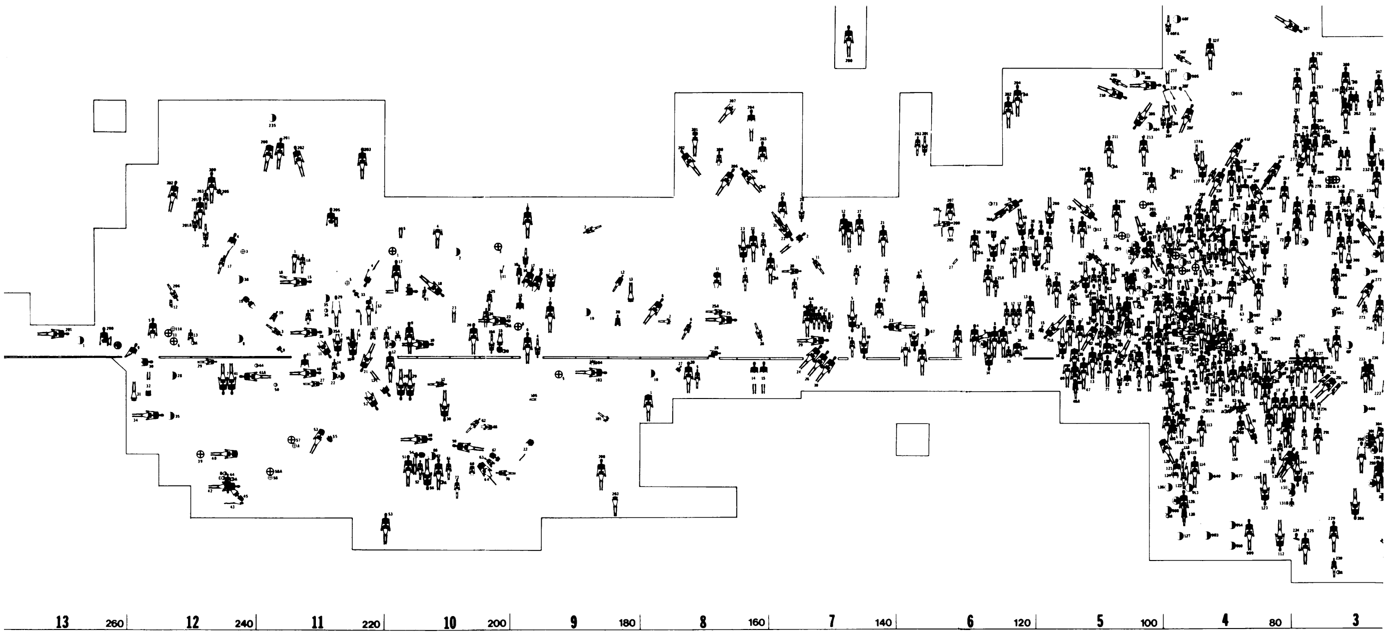


Figure 21.3 **Plan of the prehistoric Libben site, Ottawa County, Ohio.** Studies of skeletal populations such as this one can lead to insights into demographic aspects of early human populations. The area in bold outline is a blowup of part of the plot. From Lovejoy et al. (1985a).

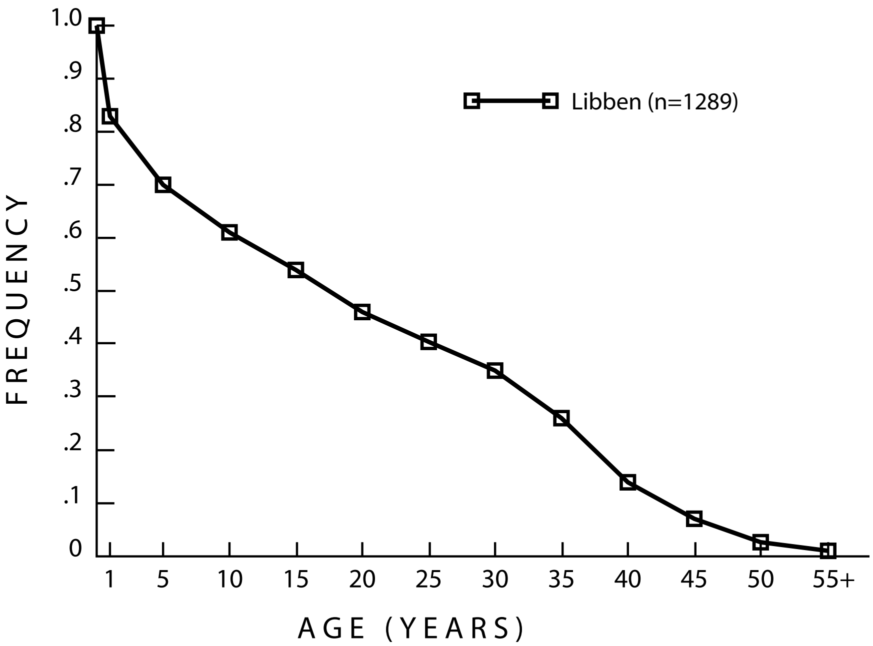
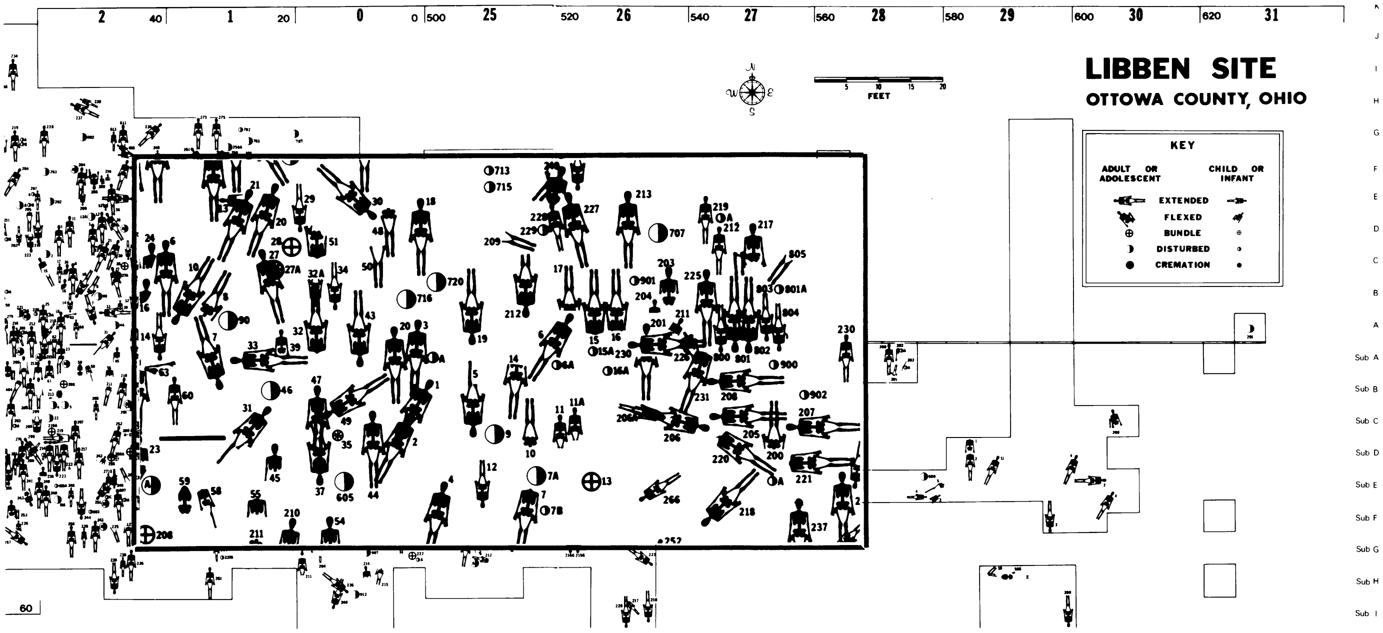


Figure 21.4 **Survivorship curve based on the prehistoric Libben skeletal population.** Data from Lovejoy et al. (1977).



In traditional paleodemography, the calculations involved in demographic reconstructions from skeletal remains are quite simple (*e.g.,* Ubelaker, 1989). For example, consider survival through time, beginning with live births. At birth, survival would be 100%. By age 5, with high infant mortality, perhaps only 60% of the original population would have survived. This would mean that 40% of the cemetery population would have been made up of children in the 0- to 5-year-old age range. By plotting the age estimates for these and the other burials in 5-year intervals through time, one could reconstruct a survivorship curve for the population (see Figure 21.4), examine survivorship by sex, or make deductions about life expectancy in the population. Meindl et al. (2008), however, point out that paleodemographic reconstruction is not this simple; rates of intrinsic population growth, female total fertility rate, and the incidence of infanticide, all of which are interrelated, must also be taken into account.

Bocquet-Appel and Masset (1982) were among the first to take a critical look at the practice of traditional paleodemography. They noted that the age-at-death profiles of prehistoric populations are artifacts of the age distributions of the modern skeletal collections upon which skeletal aging methods are based. They also noted that the low correlation between skeletal age and chronological age in humans leads to an inherent inaccuracy in all skeletal age estimates. Over the next two decades, concerns about the inherent assumptions of traditional paleodemography and the validity of traditional paleodemographic methodologies continued to grow.

In 1999, an international workshop to address many of these concerns was held in Rostock, Germany (Hoppa and Vaupel, 2002). The result was the "Rostock protocol," a set of methodological improvements to paleodemography that can correct for age biases using maximum likelihood analysis and Bayesian inversion to produce unbiased age estimates.

It is important to be able to derive demographic information about past human groups. One must note, however, that accurate and reliable demographic reconstruction can only be achieved when all of the required parameters are known or can be reasonably estimated. Most archaeologically derived skeletal samples do not meet the conditions of the imaginary example given above, and survivorship curves that they generate are prone to systematic error as a result. For example,

many human groups differentially dispose of the dead. If there is bias in their burial practices, the demographic profile of that population cannot be determined accurately. Many cemeteries show differential preservation that favors young adult individuals over children or elderly adults because bones of the former are stronger and less prone to destruction by taphonomic agents [evidence for bias due to preservation can be found by careful analysis of the sample (Walker et al., 1988)]. Many cemeteries are excavated nonrandomly or are sampled incompletely. Only intact specimens are saved subsequent to collection in many archaeological excavations. Many skeletal samples are curated poorly, with the loss of much material. In short, most archaeologically derived skeletal populations are inadequate to provide accurate paleodemographic reconstructions. If an understanding of paleodemographic aspects of ancient populations is the goal of a research project, it is imperative that the osteologist work closely with the archaeologist to ensure that sampling strategy does not bias the ultimate results.

Waldron (1991: 24) expresses the linkages and pitfalls of studying demography and disease in skeletal populations as follows:

> *The underlying assumption that is inherent in any attempt to use a death assemblage to predict something about the living is that the dead population is representative — or at least typical — of the live population. Given all the non-random events that surround death and burial, not to mention preservation and recovery, this is at best an approximation, and at worst the two (the live and the dead) bear no epidemiological relation to each other whatsoever. However, it is clearly important to know where on this spectrum a particular group, or set of groups, lies, especially if the data derived from their study are to be used to construct life tables, to make inferences about changing patterns in disease or dietary habits, or to draw any of the other demographic conclusions that are so commonly bandied about.*

The relationship between adoption/intensification of agriculture and population size and health has been an object of anthropological inquiry for several decades. Paleodemographic and paleopathological data have been brought to bear on this subject for many years, and in the early 1990s, the idea that agriculture brought with it a decreased quality of life and increased mortality rates was widely accepted. Then, in a sobering and influential contribution, Wood and colleagues (1992) reminded anthropologists that the study of prehistoric populations and their health is a complex undertaking, never straightforward or simple. These authors question a basic assumption made by many osteologists concerning lesions found on skeletal remains. They argue that rather than reflecting declining community health, such lesions indicate that the affected individuals survived some disease, that such survival might actually indicate an *improvement* in health, and that individuals who lived long enough to manifest pathological lesions on their skeletons were advantaged relative to people who succumbed to disease before their skeletons were affected. Furthermore, these authors note that large numbers of immature skeletons may indicate more about fertility than mortality. These observations are in sharp contrast to the received wisdom in paleopathology and paleodemography. How, then, are osteologists to interpret paleopathology on a populational basis? Wood et al. (1992) considered the skeletal evidence pertaining to the transition from hunting and gathering to settled agriculture to be equally consistent with either an improvement or a deterioration of health (see also Cohen, 1994), concluding that considerably more critical research is required. Nearly a decade ago the "Global History of Health Project," an ambitious meta-project to facilitate the collection of standardized indicators of health, was launched. Based on the data produced in the first years of this project, Larsen (2006) concluded that "the change in diet and acquisition of food resulted in a decline in quality of life for most human populations in the last 10,000 years" (see also Gibbons, 2009).

Applying human skeletal data from historic and prehistoric contexts to important questions about culture and biology is an important avenue of anthropological investigation. Decades of such application have brought an increased understanding of the complexities involved in such studies. It is clear that anthropologists will continue to use skeletal populations in efforts to better understand the past and will do so with increasingly sophisticated techniques and heightened cautions built upon a better appreciation of the fragmentary and biased nature of the records that they study.

Suggested Further Readings

Bailey, S. E., and Hublin, J.-J. (Eds.) (2007) *Dental perspectives on human evolution: State-of-the-art research in dental paleoanthropology.* New York, NY: Springer. 409 pp.

Detailed volume on dental morphology, variation, pathology, and wear in modern and ancient populations. Techniques such as neural network analysis, micro-CT, and strontium-calcium ratio analysis are explored.

Bocquet-Appel, J.-P. (Ed.) (2008) *Recent advances in palaeodemography: Data, techniques, patterns.* Dordrecht, Netherlands: Springer. 294 pp.

Current methods and tools used in paleodemography are explored through papers that were presented at the 25th World Population Conference.

Chamberlain, A. T. (2006) *Demography in archaeology.* Cambridge, UK: Cambridge University Press. 256 pp.

Review of current methods used in the study of demography. Includes techniques used in exploring historic, ethnographic, and archeological lines of evidence.

Hoppa, R. D., and Vaupel, J. W. (2002) *Paleodemography: Age distributions from skeletal samples.* New York, NY: Cambridge University Press. 276 pp.

An important edited volume that introduces the Rostock protocol for obtaining unbiased age estimates, as well as other modern paleodemographic techniques.

Howells, W. W. (1989) Skull shapes and the map: Craniometric analyses in the dispersion of modern *Homo*. *Papers of the Peabody Museum of Archaeology and Ethnology* 79:1–189.

This monograph by the dean of craniometric analyses assesses the evolutionary divergence in cranial shape among different geographic areas.

Katzenberg, M. A., and Saunders, S. R. (2008) *Biological anthropology of the human skeleton* (2nd ed.). New York, NY: Wiley-Liss. 680 pp.

Part 4 (Chemical and Genetic Analyses of Hard Tissues) and Part 5 (Quantitative Methods and Population Studies) of this edited volume are of special interest.

Larsen C. S. (1997) *Bioarchaeology: Interpreting behavior from the human skeleton*. Cambridge, UK: Cambridge University Press. 461 pp.

A comprehensive summary of all aspects of bioarchaeology: the standard volume in the field.

Lewis, M. (2009) *The bioarchaeology of children: Perspectives from biological and forensic anthropology.* Cambridge, UK: Cambridge University Press. 268 pp.

An introduction to the osteology, paleopathology, and paleodemography of children.

Mays, S. (2010) *The archaeology of human bones* (2nd ed.). London, UK: Routledge. 432 pp.

Focuses on the analysis of bones from archaeological contexts. Includes a chapter dedicated to DNA analyses, as well as a chapter on isotope studies.

Mellars, P., Boyle, K., Bar-Yosef, O., and Stringer, C. (Eds.) (2007) *Rethinking the human revolution: New behavioural and biological perspectives on the origin and dispersal of modern humans.* Oakville, CT: McDonald Institute for Archaeological Research. 436 pp.

A compendium of current research including advances in demographic theory, presented at the 2005 conference "Rethinking the Human Revolution."

Scott, G. R., and Turner, C. G. (1997) *The anthropology of modern human teeth: Dental morphology and its variation in recent human populations.* New York, NY: Cambridge University Press. 382 pp.

A comprehensive look at how teeth can be used to assess population biology.

Teaford, M. F. (1991) Dental microwear: What can it tell us about diet and dental function? In: M. A. Kelley, and C. S. Larsen (Eds.) *Advances in dental anthropology.* pp. 341–356. New York, NY: Wiley-Liss.

This paper summarizes work on the microwear of mammalian teeth, providing a good summary of the accomplishments and goals of using dental microwear to establish diet in extant and skeletal populations.

Ubelaker, D. H. (2008) *Human skeletal remains: Excavation, analysis, interpretation* (illust. ed.) New Brunswick, NJ: Aldine Transaction. 146 pp.

Chapter 5 provides a concise review on prehistoric population dynamics.

Ungar, P. S. (Ed.) (2007) *Evolution of the human diet: The known, the unknown, and the unknowable.* New York, NY: Oxford University Press. 413 pp.

A recent survey of the current state of research into prehistoric diets.

Verano, J. W., and Ubelaker, D. H. (Eds.) (1992) *Disease and demography in the Americas.* Washington, DC: Smithsonian Institution Press. 294 pp.

An edited volume to commemorate the Columbus Quincentenary by examining the effects of Europeans contacting New World populations. The contributions of skeletal studies to this field are summarized by leading experts for all regions of North and South America.

Waldron, T. (1994) *Counting the dead: The epidemiology of skeletal populations.* West Sussex, UK: John Wiley and Sons. 124 pp.

An excellent introduction and critical evaluation, useful in paleodemography and paleopathology.

Waldron, T. (2007) *Paleoepidemiology: The measure of disease in the human past.* Walnut Creek, CA: Left Coast Press. 150 pp.

A clear and approachable introduction to the concepts of epidemiological analysis in an archaeological context.